

SPATIAL DISTRIBUTION OF A LEAF-EATING
SAHARAN GERBIL (*PSAMMOMYS OBESUS*)
IN RELATION TO ITS FOOD

by

Martin DALY and Sandra DALY*

La distribution spatiale des *Psammodomys* dépend de celle de leur nourriture, les feuilles des Chénopodiacées. Les femelles adultes habitent les endroits où les vivres sont les plus abondants. Elles gardent entre elles un certain éloignement, ce qui a une réelle signification quand la nourriture manque. Le choix du site d'habitat des mâles dépend des habitats des femelles.

I. INTRODUCTION

Gerbils inhabit deserts and semi-deserts, and live at relatively low densities for small rodents (Petter, 1961). Most species are aggressively solitary (Kirchshofer, 1958 ; Petter, 1961 ; Prakash & Jain, 1971 ; Daly & Daly, 1974), but concentrations are found in suitable habitat. Therefore, gerbils have been called both "territorial" and "colonial". These two labels are not immediately reconcilable, for the former implies a non-random degree of spacing between individuals, whereas the latter implies clumping.

Spacing and clumping could be manifest on different scales in the same spatial data. If the scale is made large enough, we must eventually find non-random clumping, if only because a species occurs in suitable habitat, and is absent elsewhere. "Colonialism" implies more : a non-random clumping within suitable habitat, a clumping that depends on social motives, and does not merely reflect the non-random distribution of some resource.

The question of clumping *vs* spacing can therefore be phrased : "Are individuals more or less aggregated than one would expect by chance, *given* the influence of resource distribution ?". Any answer must be based on data on the distribution of animals and relevant resources, and, moreover, on a model or procedure to generate, from the resource distribution, an expected (chance) degree of scatter of animals. This paper presents such an analysis for a small population of one gerbil species, *Psammodomys obesus*, and one resource, its food.

* C.N.R.S., Centre de Recherches sur les Zones Arides, Beni-Abbès, Algérie, and Department of Psychology, University of Bristol.

P. obesus, the sandrat, is ideally suited for such a study. It is a diurnal and sedentary species, easily trapped, marked, and observed (Daly & Daly, 1974). It is furthermore a food specialist, feeding almost exclusively on succulent perennials of the family Chenopodiaceae (Petter, 1952; Daly & Daly, 1973). This specialization holds several advantages for this study. First, food is manifestly the critical resource at a gross level of distribution analysis: throughout its range, the sandrat occurs where chenopods are numerous, and is absent in their absence. Secondly, the resource is conspicuous and practicably measurable, unlike such foods as seeds and insects. Thirdly, problems of equating food items are minimized, for a sandrat ordinarily lives on few or even a single food species, in contrast to the omnivory of other gerbils (e.g. Prakash, 1962).

II. METHODS

A. THE STUDY AREA

The study was conducted in the northwest Sahara, at the oasis of Ouarourout (30°9'N, 2°13'W) in the region of Beni-Abbes, Algeria. Ouarourout is one of many small oases situated in the canyon of the Wadi Saoura, on the northeast bank of the wadi bottom. A diffuse but steady water supply comes from the water table in the massive Great Western Sand Sea (Grand Erg Occidental). At the east end of Ouarourout, this flow is channeled by foggaras into cisterns, whence it is used to irrigate gardens. Over most of the oasis, the water arrives and disperses by natural subterranean means; the only human modification has been the introduction of date palms. There are no permanent inhabitants; the gardeners walk the six km from Beni-Abbes daily. However, a nomad family made its camp nearby during part of this study, departing in February.

The north side of the Saoura at Ouarourout consists of six elongated zones that are distinct in their topography and vegetation. (Plant species identifications follow Ozenda, 1958.)

1. Wadi bottom. Humid clay with a sandy, salty crust. Dominant plants are a shrub or small tree, *Tamarix gallica* (Tamaricaceae), and a glasswort, *Salicornia fruticosa* (Chenopodiaceae).

2. Sandy margin. A narrow strip, generally less than 10 m wide, with small dunes of fine sand, dense *T. gallica* up to 2 m tall, and small, low bushes of *Atriplex halimus* (Chenopodiaceae).

3. Clay plateau. A band 120 to 180 m wide, with scattered bushes, up to 3 m in diameter, of *Salsola foetida* and *Suaeda mollis* (Chenopodiaceae) and *Zygophyllum album* (Zygophyllaceae), as well as rarer, smaller specimens of *A. halimus* and *Traganum nudatum* (Chenopodiaceae) and *Cressa cretica* (Convolvulaceae).

4. Sandy slope. Zone 3 lies ten to twenty m below zone 5, and is separated from it by a slope of up to about 20° , mostly covered with sand dunes, copses of a large tree, *Tamarix speciosa* (Tamaricaceae), and cultivated date palms, *Phoenix dactylifera* (Palmae). *S. mollis* is numerous, especially near the bottom of the slope. *Z. album*, *S. foetida*, and *T. nudatum* also occur.

5. Reg. A gravelly, sandy plain about 2 km broad, sparsely populated with a relatively great variety of low, bushy species. These include no Chenopodiaceae, except rare small individuals of *Cornulaca monocantha*.

6. Erg. The great dune desert.

The vegetation comprises very few species : in zones 1 to 4, one could search in vain for even a single representative of any species other than the ten listed above. Annuals were virtually absent.

These zones are readily ranked for total vegetation density (biomass per unit area) : $4 > 2 > 1 > 3 > 5 > 6$. Zone 4 owes its relative verdure to the subterranean springs in the slope, zones 1 and 2 to the low-lying permanent water table which is replenished by the Saoura's rare floods. In November 1973, there was a substantial flow, the first in seven years. On very rare occasions, such floods have inundated zone 3.

Considering only chenopods, the ranking is $4 > 3 > 2 > 1 > 5$. Sandrats occurred mainly in zone 4, frequently in 3, very rarely in 2, and never in 1 or 5.

The study area selected for quantitative survey was a rectangular strip 200×1050 m = 21 ha. It included all the main areas inhabited by sandrats and their principal food plant *Suaeda mollis*. Its breadth was roughly that of zones 3 and 4 ; its length ran from a fence enclosing the gardens in the east, to the west end of the oasis. A grid of 84 50-m squares was marked out with stone cairns erected at the corners. Once the animals' home sites were known, the entire grid was shifted 10 m, so that all occupied burrow systems would fall within squares and not on their borders. Every bush and tree within the area was mapped and named according to a rectangular coordinate system.

B. MEASUREMENT OF THE DISTRIBUTION OF ANIMALS AND FOOD

1. Measurement phases

Sandrats exploit small domains that occasionally drift or shift, and such movements sometimes follow local exhaustion of food resources (Daly & Daly, 1974). Aims of the present study were there-

fore : 1) to inter-relate the distribution of sandrats and of food, measured, as nearly as possible, at one point in time ; and 2) to seek relationships between changes in the two distributions, measured over a time period. With these objectives, two censuses were conducted, each in three phases :

- First census. Jan. 3-30, 1974.
 1. Jan. 3-18. Daily animal trapping and spotting, mostly in early morning, and daily vegetation estimation practice, mostly in late morning and early afternoon.
 2. Jan. 19-24. Vegetation estimation (*Chenopodiaceae* spp.) all day, with opportunistic animal spotting.
 3. Jan. 26-30. Trapping and spotting as in phase 1.
- Second census. Mar. 30-Apr. 11, 1974.
 4. Mar. 30-Apr. 1. As in phase 1.
 5. Apr. 2-8. Vegetation estimation (*Suaeda mollis* only), mostly in early morning, and some trapping and spotting.
 6. Apr. 9-11. As in phase 3.

2. *Animal trapping and spotting procedures.*

Sandrats were trapped in wire cage traps baited with fresh leafy stems of *S. mollis*. Trapped animals were sexed, weighed, measured, marked for permanent identification by amputation of one or two toes, and marked for visual identification by cutting patches of fur, revealing the dark underfur in distinctive patterns and loci. Animals were released at capture sites as soon as these procedures were complete. No sandrat spent more than about an hour and a half in a trap. Marked animals were subsequently identified by spotting with binoculars.

Trapping was first conducted wherever sandrats or signs of their activity were seen, and most of the animals on the study area were thus marked within three days (18 of the 24 marked in January). On subsequent days, as many marked animals as possible were spotted, and traps were set wherever an unidentified sandrat was seen, or a burrow had been used but no animal seen. When there was some doubt about whether a particular bush was in use, the sand was smoothed by hand, and later checked for tracks. After Jan. 13, no unmarked sandrat was trapped or seen until phase 4, so it was assumed that all adults present in January were marked. Similarly, all adults present for the second census were marked by April 2.

3. *Vegetation estimation procedures.*

The amount of food on a bush was assessed by visual examination by two practiced estimators. Practice was conducted on bushes in an

area uninhabited by sandrats, lying about 1 km from the study area on the opposite side of the wadi bottom. A bush or part thereof was selected for estimation and examined independently. When the two estimates were recorded, an agreed estimate was attained through discussion and further examination. Practice estimates were usually made to the nearest one or ten grams of edible growth. The bush was then carefully cut up and weighed, discarding all woody or dry parts that sandrats would reject. The edible portion is principally fleshy green leaves, but also includes soft stems, and, on some bushes, the minute flowers whose contribution to the weight is negligible.

During the actual census estimation (phases 2 and 5), estimates were made to the nearest 100 gm. When the independent estimates differed (9% of all live bushes), an agreed value was reached through discussion, further examination, and sometimes a validation check on a small bough of ten to twenty gm. Two or three such validations were made daily throughout the estimation periods. During the first census (phase 2), four of the 84 squares were assessed independently so that a correlational measure of inter-estimator reliability could be computed.

During the second census, only *S. mollis* was estimated. Other species were ignored in order to complete the survey reasonably quickly. This was necessitated by the increased plant growth, and by the heat, which forbade working all day.

III. RESULTS AND DISCUSSION

A. ANIMAL CENSUS

35 sandrats, 24 females and 11 males, were marked on or near the study area. The numbers present on the study area in each census period are shown in Table 1.

TABLE 1. — The sandrat population on the 21-ha study area

	Adults		Juveniles	
	♂♂	♀♀	♂♂	♀♀
1st census (mid-January, 1974)	3	8 (+ 4)	3	1 (+ 3)
2nd census (early April, 1974)	2	7	3	3
Mid-January, 1973	4	9		
Early April, 1973	5	12		

Numbers were evidently in a steep decline during January. The seven females, four adults and three juveniles, included parenthetically in Table 1, were all marked on the study area within the first week of January, but had disappeared when food estimation (phase 2) was begun on Jan. 19.

Seven of the eight females present at the end of phase 1 occupied small domains within single squares ; the eighth made several moves over distances up to 154 m, never staying more than a week at one site. The three adult males had larger ranges, penetrating 2, 5, and 8 squares, but all three had identifiable home burrows where they could usually be found alone early in the morning.

Six of the seven resident January females were still present in April, along with one new female. All three January males had disappeared. The two adult males in April were a large immigrant, apparently staying at a single burrow, and a younger male who had been present as a juvenile in January, and now ranged over three squares from a new home burrow. Despite the small numbers involved, there is a significant sex difference in survival of resident adults from one census to the next, on the directional hypothesis of greater turnover among males ($p = 1/30$, by the Fisher exact test for a 2×2 contingency table).

The same area was intensively trapped and observed during a behavioural study the previous winter (Daly & Daly, 1974). Table 1 includes the numbers of resident adults present on these 21 ha at the same dates in that year.

B. VEGETATION CENSUS

Table 2 presents the estimates of edible chenopod growth. The numbers of bushes include all those with any living leaves, except for very small new sprouts without woody stems.

TABLE 2. — Chenopod plants on the 21-ha study area

	<i>Suaeda mollis</i>	<i>Salsola foetida</i>	<i>Traganum nudatum</i>	<i>Atriplex halimus</i>
Number of living bushes	1,011	696	166	12
Edible growth (kg) :				
January	63.8	23.2	3.2	0.3
April	185.7			

Estimation performance gradually improved during practice phase 1. For Jan. 4-5, the mean absolute error of estimation was 51% ; for Jan. 9-10, 23% ; and for the last ten bushes at the end of phase 1, 12%. For the four squares assessed independently, inter-estimator reliability (the correlation between the two estimator's sets of scores) was 0.99.

In the second census, and in all analyses below, the only food species considered is *S. mollis*. The justification is that this was the only food of any importance for the sandrats during the study period.

This was variously evidenced. Direct observation of animals and study of tracks indicated almost no exploitation of other plants. The only burrow under another species ever used during the study was one under *S. foetida*, where an itinerant adult female was caught once. Furthermore, there was a strong relationship between the distributions of *S. mollis* and of sandrats (Fig. 1 and section D, below), a relationship that is only weakened by considering other plants.

S. mollis is the favourite food, even for those animals living under *S. foetida*; *S. mollis* can be more efficiently used than *S. foetida* or *T. nudatum*, in the sense both of quantities needed and of time costs (Daly & Daly, 1973). Analyses of the edible parts of these three species are included in the Appendix.

C. THE RELATIONSHIP BETWEEN FOOD AND ANIMAL BIOMASS

The 15 weaned sandrats present at the first census weighed 1.3 kg, 2.0% of the available *S. mollis*; the seven females who disappeared during January would bring the total to 1.9 kg, 3.0%. At the second census the 15 present totaled 1.1 kg, 0.5% of the *S. mollis* then available. These ratios of animal to vegetation biomass would be slightly higher were nursing litters included.

These are very high ratios in view of the low nutritive value of the food (see Appendix), and the high consumption necessary. Adult *P. obesus* maintained in the laboratory on an exclusive diet of *S. mollis* ate over 80% of their body weight daily, and juveniles ate over 100% (Daly & Daly, 1973). There is some evidence that similarly large quantities are consumed in the wild. One large female who occupied an isolated *S. mollis* bush outside the study area provides an example. On Jan. 9, she was in an advanced state of pregnancy at 135 gm, and fresh green growth on her bush was estimated at over 5 kg. The bush was then cropped to complete leaflessness in only 18 days. On Jan. 27, she had to move her litter over high dunes to a new burrow. This steady defoliation was unquestionably the sandrat's work; the surrounding sands remained trackless. In such dense new growth, sandrats can cut and carry several gm at a time, and excessive food gathering and some wastage probably result, for *S. mollis* blackens and spoils within a few hours.

Gradual defoliation usually takes place more slowly than in the above example. Typical food-gathering domains may contain about 2 to 6 kg of food, and it can generally be seen that the maintenance of an adult on a sustained yield is impossible. Unfortunately, we have no information on the primary productivity of *S. mollis*, nor on the

effects of harvesting upon such productivity. Food outside active domains is frequently too sparsely scattered to be exploited.

The above considerations support the conclusion that the sandrat population was falling early in the study because of a limiting food supply

The spring increase in green growth may depend in part on seasonal changes in primary productivity, but the main factor was certainly the February departure of the nomads and their domestic animals, including about fifty goats and several camels, who seldom fed for very long on the study area, but passed through it slowly on most days. Both species ate palm leaves and *S. mollis* in zone 4, and *S. foetida* and *S. mollis* in zone 3.

Gauthier-Pilters' (1961) study of camels in the Saoura shows that these large mammals can have an enormous impact on such sparse vegetation. In February, they eat up to 40 kg per animal per day when feeding in the wadi. One male ate 6.4 kg of *T. nudatum* in a single hour, twice the edible quantity on the entire study area in January 1974.

The Saoura is being rapidly defoliated by the combined effects of increasing population pressure, drought, and dams. In the 1950's, *Psammomys* densities in the wadi, and at Ouarourout in particular, were about 50 to 100 per ha in the best habitat (Petter, 1961 and personal communication). In 1972-4, extensive reconnaissance and trapping revealed none as high as 5/ha. The activities of domestic animals are reflected in changes in the species composition of the plant community as well as in the overall decline. *T. nudatum* is the camel's favourite food in the wadi, and *A. halimus* is the second choice (Gauthier-Pilters, 1961). These two chenopods are now much sparser than the less preferred *S. mollis* and *S. foetida*, although *T. nudatum* was the dominant chenopod 20 years ago (Bouzidi & Petter, personal communication); it is now represented in many areas by numerous thick woody stems bearing a few tiny leafy twigs.

D. THE SPATIAL DISTRIBUTION OF ANIMALS AND FOOD

1. *January analysis.*

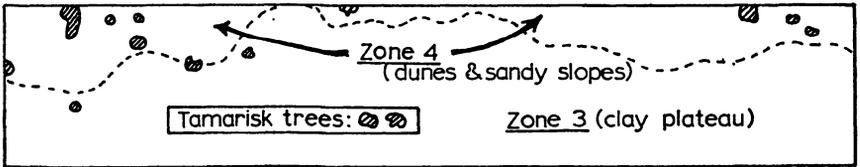
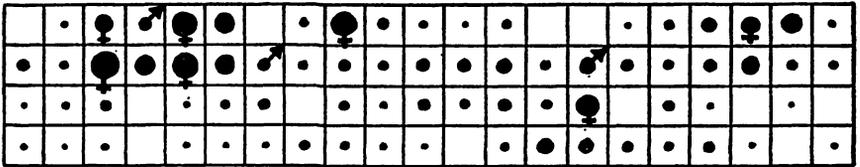
Sandrats occupied the areas with the best supplies of *S. mollis* (Fig. 1). When the 84 squares are ranked for *S. mollis* weight, squares 1, 2, 3, 4, 5, 8, 12 are inhabited by the seven resident adult females; squares 13, 15, 18 by the three males. The sex difference is significant (Mann-Whitney $U = 0$, $p = .012$).

Earlier observations (Daly & Daly, 1974) indicated that females defend food-gathering ranges from one another (and from males). We

therefore predict "spacing" rather than "clumping". The problem is to test the significance of the observed degree of spacing, given the observed influence of food distribution. This can be done with a three step procedure :

- 1) Use the data to generate probabilities of occupying squares of different food content.
- 2) Use the probabilities to randomly and independently assign the animals (in this case the seven resident females) to squares.
- 3) Compute the probability that steps 1 and 2 produce spacing equal to or greater than that observed.

January



March - April

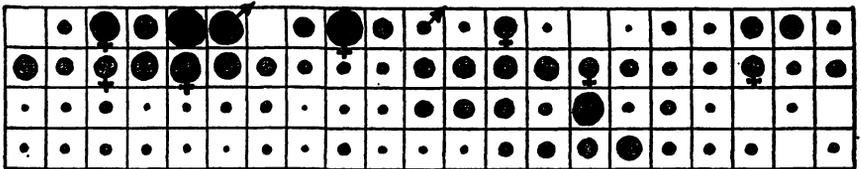


Fig. 1. — Map of the study area, and the distribution of sandrats and their food. The areas of black circles are proportional to the weight of the edible *Suaeda mollis* within each 50-m square. ♂ and ♀ mark squares containing the home burrows of established adults.

Step 1 could be carried out with any of various models. The following model uses equal-interval categories of food content ; it is just one possible analysis of this sort, arbitrarily chosen for its relative ease of calculation.

The 84 squares can be categorized as follows :

- 1) 0-1.5 kg. 71 squares. 0 female.
- 2) 1.6-3.0 kg. 8 squares. 2 females.
- 3) 3.0-4.5 kg. 5 squares. 5 females.

5/7 of females are in category 3, 2/7 in category 2, 0/7 in category 1. Using these proportions as probabilities of any individual female residing in each category, and treating all squares within a category as equally likely, we obtain :

p (as spaced as observed, i.e. no two females in one square)	= .058
joint p (as spaced as observed <i>and</i> as concentrated in best food as observed, i.e. at least 5 in category 3)	= .011
conditional p (as spaced as observed <i>if</i> as concentrated in best food as observed)	= .016

Of these, the conditional probability is the logically appropriate test of the problem as stated above. One can therefore conclude that females indeed "space" rather than "clump".

2. April analysis.

In April, the seven females inhabited squares ranked 2, 4, 7.5, 13, 15, 19, 21.5 ; the two males squares 3 and 43.5. This represents a reduced tendency to occupy the best sites, but the available *S. mollis* had trebled overall, and there was actually more food in the occupied squares than in January (Fig. 1). Six females remained from the January census, and none had moved farther than 39 m. This conservatism reflects the fact that established females were already occupying the ranges with the best sustained yields. Areas with new growth were left open to exploitation by juveniles.

As in January, no two females occupied the same square, but a significant degree of spacing is no longer demonstrable by an analysis like that used for the January data, because of the reduced concentration in the best food squares. A similar analysis, again dividing the squares into three equal-interval categories, yielded a conditional probability (as spaced as observed *if* as concentrated in best food as observed) of 0.44.

3. Sex as a factor in site selection.

Whereas food resources are the determining factor in the female's home site selection, the females are themselves a relevant resource for the male's choice. Adult males often live at central points in ranges encompassing two or more females, and visit them frequently (Daly & Daly, 1974). It was remarkable that the two adult males who lived in the denser west part of the study area in January 1974 inhabited the same two burrows and virtually the same ranges as had the two domi-

nant males S1 and 51 during the previous spring, although they were not the same animals. Likewise, all the burrows occupied by adult females in 1974 had been occupied by other adult females at some time in 1972-3.

E. TERRITORY AND COLONIALISM

The demonstration of spacing rather than clumping in January suggests a territorial rather than colonial social organization, at least when populations approach food limits. However, it has proved difficult to observe "territorial behaviour" according to any rigorous definition: dominance does not often appear to be locus-dependent (Daly & Daly, 1974). Aggressiveness and sedentariness can together produce a "territorialism" functionally similar to the effects of reversible locus-dependent dominance, but "territories" are often taken from their holders.

If a territory is an area from which like-sexed conspecifics are (more or less) excluded, female ranges can be called territories, but male ranges cannot, for although males are certainly mutually aggressive, exclusion does not result (Daly & Daly, 1974). Extensive and even total overlap of adult male ranges also occurs in other gerbils, including *Meriones* spp. (Daly & Daly, in preparation). Although a great deal has been written about "territorial scent-marking" in the male Mongolian gerbil *Meriones unguiculatus* (e.g. Thiessen, 1973), there is no evidence that this behaviour, performed by many gerbils including sandrats (Sokolov & Skurat, 1966; Daly & Daly, 1974), serves such a function.

The 50-m square used in this study represents no limit to tolerated proximity. In fact, the shortest distances observed between adult females' burrows were 24 m in 1974, and 14 m in 1973. Still nearer neighbours must be tolerated when densities approach 100/ha (Petter, 1961). Conversely, where food is very sparse, an adult female's range can greatly exceed anything observed at Ouarourout (Daly & Daly, in preparation).

The question remains whether colonialism can be detected on a larger scale. We think not. All along the Saoura, sandrats occur at predictable densities wherever there are chenopods, often in surprisingly isolated places. Where there is substantial new growth, there may be a lag in invasion, so that a clumped distribution appears temporarily. This is hardly the sort of affiliative process implied by "colonialism".

Poulet (1972) approached the spatial distribution of another gerbil, *Taterillus pygargus* of Senegal, rather differently. He concluded that

there were "micropopulations" that were reproductive units, called them evidence of a primitive social structure, and strongly implied that a degree of social attraction is demonstrated thereby. However, no statistical demonstration of non-random clumping was attempted, nor was there consideration of the influence of resource distribution upon animal distribution; moreover, Poulet remarked that the groupings were transient and consisted primarily of undispersed siblings. Thus, although one might conclude from a first reading that *T. pygargus* is a truly colonial gerbil, it is not yet clear whether its social system differs at all from that of *P. obesus*.

ACKNOWLEDGMENTS

This research was supported by a grant to John Crook from the Science Research Council of Britain. The CRZA very generously provided accommodation and facilities at Beni-Abbès; we thank in particular the director, Jean Marçais, and the station chief, Bachir Kebir.

APPENDIX

For the following analyses, we thank Prof. P. Binet, Université de Caen; they were conducted under the cadre of the Equipe de Recherche Associée N° 405 of the CNRS, with the technical assistance of Jacques Bigot and Monique Duymé. The materials were the edible leaves and stems of plants collected at Ouarourout in April 1973.

	<i>Suaeda mollis</i>	<i>Salsola foetida</i>	<i>Traganum nudatum</i>
% of fresh weight : water	88.1	85.0	84.0
% of dry weight : N (total)	4.6	2.9	3.6
(in protein)	2.8	1.9	2.5
(in free amino acids)	0.4	0.1	0.2
Soluble sugars (total)	4.9	1.8	2.4
(reducible)	3.9	0.4	0.6
Starch	0.2	0.0	0.4
Cellulose	8.7	9.0	11.2
Na	12.2	11.8	7.8
K	1.6	3.8	3.9
Ca	0.6	1.0	1.1
Mg	1.4	2.1	2.4
Cl	7.1	3.8	1.0
P	0.2	0.2	0.2

SUMMARY

The relationship between the spatial distributions of a leaf-eating gerbil (the sandrat, *Psammomys obesus*) and its food was studied in the northwest Sahara. All sandrats on a 21-ha study area were trapped and marked, and their home burrows and ranges determined. All food plants were examined and their edible weight estimated in January and again in April.

Adult females occupied the best food sites. They maintained a degree of spacing from one another, which was demonstrably non-random in January when food was scarce. For male site selection, the females are themselves a relevant resource.

Present address : 7 Greengate Rd.,
Don Mills, Ontario, M3B 1E7, Canada.

BIBLIOGRAPHY

- DALY, M., and S. DALY, 1973. — On the feeding ecology of *Psammodmys obesus* (Rodentia, Gerbillidae) in the Wadi Saoura, Algeria. *Mammalia*, 37 : 545-561.
- DALY, M., and S. DALY, 1974. — Behaviour of *Psammodmys obesus* (Rodentia Gerbillinae) in the Algerian Sahara. *Z. Tierpsychol.* (in the press).
- DALY, M., and S. DALY, *in preparation*. — Socio-ecology of Saharan gerbils.
- GAUTHIER-PILTERS, H., 1961. — Observations sur l'écologie du Dromadaire dans le Sahara Nord-Occidental. *Mammalia*, 25 : 195-280.
- KIRCHSHOFER, R., 1958. — Freiland- und Gefangenschaftsbeobachtungen an der nordafrikanischen Rennmaus, *Gerbillus nanus garamantis* Lataste 1881. *Z. Säugetierk.*, 23 : 33-49.
- OZENDA, P., 1958. — *Flore du Sahara*. C.N.R.S., Paris.
- PETTER, F., 1952. — Note préliminaire sur l'éthologie et l'écologie de *Psammodmys obesus* Cretzschmar. *Mammalia*, 16 : 136-147.
- PETTER, F., 1961. — Répartition géographique et écologie des rongeurs désertiques. *Mammalia*, 25, n° spéc. : 1-222.
- POULET, A. R., 1972. — Caractéristiques spatiales de *Taterillus pygargus* dans le Sahel sénégalais. *Mammalia*, 36 : 579-606.
- PRAKASH, I., 1962. — Ecology of the gerbils of the Rajasthan desert. *Mammalia*, 26 : 311-331.
- PRAKASH, I., and A. P. JAIN, 1971. — Some observations on Wagner's gerbil, *Gerbillus nanus indus* (Thomas), in the Indian desert. *Mammalia*, 35 : 614-628.
- SOKOLOV, W., and L. SKURAT, 1966. — A specific midventral gland in gerbils. *Nature (London)*, 211 : 544-545.
- THIESSEN, D. D., 1973. — Footholds for survival. *Amer. Scientist*, 61 : 346-351.

